African Invertebrates Vol. 48 (1) Pages 169–191 Pietermaritzburg April, 2007

New chironomid flies in Early Cretaceous Lebanese amber (Diptera: Chironomidae)

Isabelle Veltz[1], **Dany Azar**[2] and **André Nel**[3]*

[1]Université de Reims-Champagne-Ardennes, Groupe d'Etude sur les Géomatériaux et Environnements Naturels et Anthropiques (G.E.G.E.N.A.) E.A. 3795; Centre de Recherches en Environnement et Agronomie (C.R.E.A.), 2 Esplanade Roland Garros, Reims, 51100 France; isabelle.veltz-balatre@laposte.net; [2]Lebanese University, Faculty of Sciences II, Department of Biology, Fanar Matn P.O. Box 26110217, Lebanon; azar@mnhn.fr; [3]CNRS UMR 5143, Muséum National d'Histoire Naturelle, Entomologie, 45 Rue Buffon, Paris, F–75005 France; anel@mnhn.fr;
*Corresponding author

ABSTRACT

The oldest representatives of the Tanypodinae (Macropelopiini, Pentaneurini and Anatopyniini), *Libanopelopia cretacica* gen. et sp. n., *Cretapelopia salomea* gen. et sp. n., *Wadelius libanicus* gen. et sp. n.; the oldest representative of the Orthocladiinae, *Lebanorthocladius furcatus* gen. et sp. n.; and the oldest representatives of the Prodiamesinae, *Libanodiamesa deploegi* gen. et sp. n. and *Cretadiamesa arieli* gen. et sp. n., are described from the Early Cretaceous Lebanese amber. The male of the podonomine *Libanochlites neocomicus* Brundin, previously known only from a female specimen, is described, supporting its allocation to this subfamily. The positions of the previously described Mesozoic taxa attributed to the Chironomidae are discussed. In particular, *Gurvanomyia rohdendorfi* Hong from the Early Cretaceous of China, and *Manlayamyia dabeigouensis* Zhang from the Late Jurassic of China are considered as Diptera *incertae sedis*. The most recent discoveries demonstrate the great antiquity of the recent chironomid subfamilies and tribes and the high morphological stability within this group since the Early Cretaceous.

KEY WORDS: Diptera, Chironomidae, Orthocladiinae, Podonominae, Prodiamesinae, Tanypodinae, Early Cretaceous, Lebanese amber, aquatic, oldest records.

INTRODUCTION

Chironomid flies are common to the Jurassic and Early Cretaceous aquatic insect assemblages (Evenhuis 1994; Sinitshenkova 2002), even if the systematic positions of some of the described taxa remain debatable. Among others, *Gurvanomyia rohdendorfi* Hong, 1992 from the Early Cretaceous of China is based on an adult of unknown sex (genitalia and antennae either unpreserved or poorly preserved) (Hong *et al.* 1992). The original drawing clearly does not correspond to the original photograph. In addition, its allocation to the Chironomidae is not sufficiently supported and thus we consider it to be a Diptera of uncertain position. It will be necessary to re-examine the holotype to clarify its position. *Manlayamyia dabeigouensis* Zhang, 1991 (in fossil genus *Manlayamyia* Kalugina, 1980), from the Late Jurassic of China, is based on male and female adults, and pupae (Kalugina 1980*a*). The allocation of fossil pupae and adults to the same species of chironomid fly is strongly debatable. In this material, originally illustrated by Zhang (1991), the wing venation and body structures crucial in identifying the specimen as a chironomid, rather than a ceratopogonid, are not visible or poorly preserved. Thus, as in the case with *Gurvanomyia rohdendorfi* Hong, 1992, the allocation of *Manlayamyia dabeigouensis* Zhang, 1991 to the Chironomidae remains uncertain. It is a Diptera of uncertain position. *Sinoryctochlus insolitus* Zhang, 1991 (in fossil genus

Sinoryctochlus Zhang, 1991), from the Late Jurassic of China, is based on male and female adults, which, according to the original illustrations by Zhang (1991), have rather poorly preserved wing venation. Kalugina (1985) attributed three new species to the Middle/Late Jurassic genus *Ulaia*, i.e. *U. magna*, *U. montana*, and *U. reducta*, all based on more or less complete pupae. Their allocation to the same genus is very debatable because the pupae lack the genital structures necessary for accurate identification. Similarly, Kalugina (1985) attributed two new species to the Middle/Late Jurassic genus *Jurochlus* Kalugina, 1985, viz. *J. sibiricus* and *J. rigor*, both based on more or less complete pupae. Thus, their allocation to the same genus is also very debatable. Kalugina (1985) also placed her *U. mixta* in the Middle Jurassic genus *Ulaimailonia* Kalugina, 1985 based on a larval specimen, which is difficult to compare to the fossil pupae attributed to *Ulaia*. Finally, Kalugina (1985) described six species in the Early/Middle Jurassic genus *Podonomius* Kalugina, 1985, viz. *P. tugnuicus*, *P. splendidus*, ?*P. simplex*, ?*P. rotundatus*, ?*P. minimus*, and ?*P. undulatus*. Some descriptions are based on adult specimens while others are based on pupae. These allocations may be inaccurate since it is not possible to effectively compare adult specimens with immature instars.

Nevertheless, some specimens of Late Jurassic or Cretaceous Chironomidae are attributed to recent subfamilies, and in some cases, recent tribes. Among others, the recent subfamily Podonominae is represented by *Libanochlites neocomicus* Brundin, 1976 from the Early Cretaceous Lebanese amber. Some other taxa are also currently attributed to this subfamily, although they are more poorly preserved in lacustrine deposits. Thus, Kalugina (1985) described five new Middle/Late Jurassic species in the fossil genus *Oryctochlus* Kalugina, 1985, viz. *O. affinis*, *O. longilobus*, *O. minor*, *O. minutus* and *O. vulcanus*. Kalugina allocated certain larvae, pupae and adults to a particular species. This deduction is strongly debatable, since it is not possible to compare larval, pupal and adult characters. In addition, the adult specimens are not very well preserved. *Oryctochlus contiguus* Zhang, 1991, from the Late Jurassic of China, is based on both male and female adults, better preserved than those of *M. dabeigouensis*. Thus it is likely that this species is a true chironomid. The recent subfamily Aphroteniinae is represented by *Electrotenia* Kalugina, 1980, with one species *E. brundini* Kalugina, 1980, based on an adult male and female from the Late Cretaceous Taymir amber from North Siberia (Kalugina 1980*b*). The recent subfamily Diamesinae is represented by *Cretodiamesa* Kalugina, 1976, with one species *C. taimyrica* Kalugina, 1976, based on an adult male and female from Late Cretaceous Taimyr amber (Kalugina 1976). The recent subfamily Orthocladiinae is represented by *Metriocnemus cretatus* Boesel, 1937, *Smittia veta* Boesel, 1937 and *Spaniotoma conservata* Boesel, 1937 from the Late Cretaceous Canadian amber (Boesel 1937). However, all of these genera now have a different content and definition, with *Spaniotoma* regarded as a *nomen dubium*.

The Mesozoic Tanypodinae are represented by more uncertain taxa. Kalugina (1985) described *M. pallida* in the Middle Jurassic genus *Mailonia* Kalugina, 1985, based on a pupa. She described *T. stygialis* in the Middle Jurassic genus *Tophocladius* Kalugina, 1985, based on adults, and attributed it to the tanypodine tribe Macropelopiini. This tribal allocation is weakly supported as these fossils do not show the tarsal structures and the position of the cubital fork characteristic of Macropelopiini. Kalugina made no comparisons with the recent tanypodine genera. She also placed her "*T*". *gorchonensis* in the Middle Jurassic genus "*Tanypodites*" Kalugina, 1985, based on a very incomplete adult male, thus attributing it to the ?Tanypodinae. Kalugina (1986) described the fossil genus *Gurvanomyia* with two species, *G. magna* and *G. moderata*, from the Late Jurassic/Early Cretaceous of Mongolia, based on incomplete adults with poorly preserved wing venation. Kalugina (1986) also described *Shinlustia irae* from the Early Cretaceous of Mongolia on the basis of a poorly preserved adult.

Although the Chironomidae are not rare in the early Cretaceous Lebanese amber (Azar 2000), to date only one genus and species has been described. Herewith we describe the first fossil representatives of the Pentaneurini (Tanypodinae), the oldest representatives of the Orthocladiinae and Prodiamesinae, and the male of the podonomine genus *Libanochlites*, previously known only from a female specimen. The Mesozoic taxa currently attributed to the Tanypodinae cannot be compared with our material since those previously described taxa are all based on poorly preserved fossils.

MATERIAL AND METHODS

The studied specimens originate from the various outcrops of Lebanese amber (Azar 2000). Amber pieces were embedded in epoxy resin. All types and other examined specimens are provisionally deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN).

We follow the body and wing venation terminology of Oliver and Dillon (1989).

TAXONOMY

Family Chironomidae Newman, 1834

Subfamily Tanypodinae Skuse, 1889 (see Spies 2005)

Tribe Pentaneurini Hennig, 1950 or Macropelopiini Zavrel, 1929

Genus **Libanopelopia** gen. n.

Etymology: After Lebanon and the recent genus *Telopelopia*.

Type species: *Libanopelopia cretacica* sp. n., by present designation.

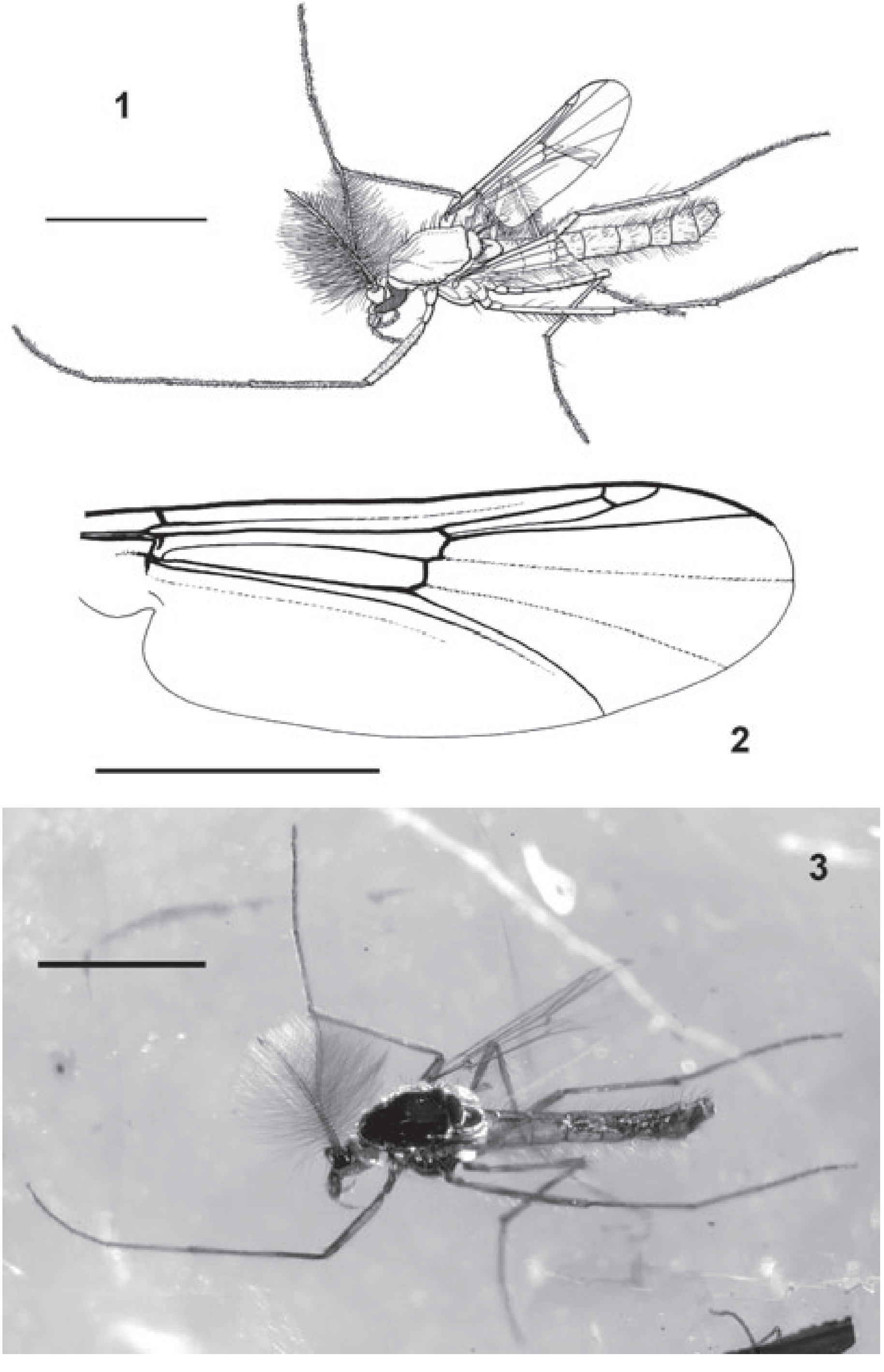
Diagnosis. Eye bare. Costa produced beyond R_{4+5} by a distance less than the length of cross-vein RM, ending slightly before M_{1+2}; R_{2+3} well separated from R_1 and R_{4+5}, apically divided into R_2 and R_3, with R_2 rather long and well distinct. Hind tibial comb disposed in one row; two tibial spurs on both mid and hind leg with lateral comb-like teeth, outer tibial spur half as long as inner spur, those of hind legs not flattened. Inferior volsella small or absent; gonostylus distinctly shorter than gonocoxite.

Libanopelopia cretacica sp. n.

Figs 1–3

Etymology: After the Cretaceous period.

Description: Head deformed, 0.4 mm long. Ocelli absent. Antenna 0.88 mm long, much longer than head, distinctly hairy; scape broad and short, rounded; pedicel very short; 14 flagellomeres, flagellomeres 1–13 covered with long setae (shortest 0.01 mm long, longest 0.48 mm long), flagellomere 13 very long (0.5 mm), flagellomere 14 evenly tapering from base to apical nipple, twice as long as broad at base. Eye bare, deformed



Figs 1–3. *Libanopelopia cretacica* gen. et sp. n., holotype HAR 2: (1) details of general habitus; (2) wing; (3) general habitus. Scale bars = 1 mm in Figs 1, 3 and 0.5 mm in Fig. 2.

but with an apically expanded dorso-medial extension, with 4 rows of ommatidia at minimum width. Clypeus 0.14 mm long, with few dorsal setae. Mouthparts lacking functional mandibles; all palpomeres with numerous setae, but the second with 2 distinctly longer setae. No postocular setae; 5 or 6 long frontal setae; inner vertical and outer vertical setae not visible.

Thorax 0.7 mm long, 0.33 mm wide, 0.5 mm high; postnotum bare, with a very distinct longitudinal median groove; scutellum bare but with 8 long setae on its posterior margin; scutal tubercle absent; 1 supraalar, 3 prealars, a series of 7 or 8 anterior acrostichals, a series of few aligned dorsocentrals; postanepisternal setae absent.

Wing macropterous, 1.44 mm long, 0.48 mm wide, hyaline, covered with macrotrichia. Costa ending just beyond insertion of last branch of radius, produced by 0.06 mm, shorter than cross-vein RM, ending slightly before M_{1+2}. Radius with 3 branches R_1, R_{2+3}, and R_{4+5}; R_{2+3} well separated from R_1 and R_{4+5}, R_{2+3} apically forked into R_2 and R_3; R_2 0.04 mm long, ending in R_1, R_3 0.1 mm long, ending in costa. Only M_{1+2} and M_{3+4} present; cross-vein MCu present; cross-vein RM 0.04 mm distal of MCu; cubital fork 0.02 mm proximal to cross-vein MCu. Anal vein An_2 absent. Halter 0.22 mm long.

Fore femur length 0.72 mm, tibia 0.82 mm, tarsus 1.06 mm; mid femur 0.71 mm, tibia 0.66 mm, tarsus 0.9 mm; hind femur 0.54 mm, tibia 0.70 mm, tarsus 0.96 mm. Tibial spur formula 1–2–2, all with lateral teeth, comb-like; those of hind legs not flattened – a state similar to extant *Derotanypus* (see Murray & Fittkau 1989, fig. 5.13D); 2 hind-leg tibial spurs, 0.04 mm and 0.02 mm long respectively. Fourth tarsomeres of all legs cylindrical, not cordiform. Middle leg claw simple as in front and hind legs; not pectinate. Hind tibial comb disposed in 1 row.

Abdomen 1.6 mm long, 0.24 mm wide. Gonostylus nearly bare, strongly curved, short, 0.07 mm long, 0.03 mm wide, distinctly shorter than gonocoxite; gonocoxite 0.12 mm long, 0.06 mm wide, with numerous long setae. Anal point very smooth, broad and small (0.7 mm wide at base, 0.02 mm deep?). Inferior volsella not visible; if present, very small.

Holotype: ♂ HAR 2. LEBANON: *South Lebanon district* [*Mouhafazit Loubnan el-Janoubi*]: Caza Jezzine, locality between villages Homsiyyeh, Aazour and Roum; Early Cretaceous, Neocomian sandstone (D. Azar coll.).

Note: This amber outcrop was discovered in July 1999 by one of the authors (D.A.), but biological inclusions were only found when the exact layer bearing amber was located in June 2004. The present chironomid fly is the first fossil insect to be described from this outcrop.

Discussion: According to the key to dipteran families (McAlpine 1981), this fossil can be included within Chironomidae because of the combination of the following characters: anal vein An2 absent; radius with only three branches R_1, R_{2+3}, and R_{4+5}, costa ending just beyond insertion of last branch of radius; ocelli absent; antennae much longer than head, and distinctly hairy; wings narrow; only M_{1+2} and M_{3+4} present; mouthparts lacking functional mandibles; postnotum with a very distinct longitudinal groove. According to the Nearctic genera keys of Oliver (1981) and the key to Holarctic subfamilies of Oliver and Dillon (1989) and to Palaearctic subfamilies in Sæther *et al.* (2000), this fossil belongs to the subfamily Tanypodinae because of the combination of the following characters: macropterous, wing extending posterior to first abdominal segment; cross-vein MCu present; R_{2+3} present, apically forked into R_2 and R_3; postnotum with longitudinal groove; wing covered with macrotrichia.

Sæther (2000*a*) proposed a phylogeny of the chironomid subfamilies. He considered the Tanypodinae as a part of the semifamily Tanypodoinae (= Tanypodinae + Usambaromyiinae + Podonominae + Aphroteniinae), mainly characterised by the presence of a gonotergite in male adults formed by the fusion of tergite IX, laterosternite IX and sternite IX. Unfortunately, the laterosternite IX is not visible in our fossil.

Nevertheless, the specimen can be attributed to the clade (Tanypodinae + Usambaromyiinae) because it shows the main synapomorphy, i.e. "tibial spurs with lateral teeth, comb-like" (Sæther 2000*a*). Affinities with the Usambaromyiinae (Andersen & Sæther 1994) can be excluded because of the presence of vein MCu, tarsomere 4 elongate and not cordiform, and claw of middle legs simple, as in front and hind legs and not pectinate.

Ansorge (1999) proposed a fossil Liassic subfamily Aenneinae, also known from the late Triassic (Krzemiński & Jarzembowski 1999), based on the presence of a long basal part of Rs (plesiomorphy), not present in our fossil. Ansorge (1999) considered Aenneinae to be a possible sister group of a clade comprising other chironomid subfamilies; however, he appears to have ignored the Telmatogetoniinae and some other subfamilies.

Kalugina (1993) erected the Cretaceous fossil subfamily Ulaiinae, based on the genus *Ulaia*, with three species, *U. communis* (pupa and an adult wing), ?*U. magna* (pupa), and *U. kangilica* (pupa). As it is impossible to rear a fossil pupa, the allocation of a pupa and an adult wing to the same species is problematic. The wing attributed to *U. communis* is of a tanypodine-type. It differs from our fossil in that its R_2 is longer than R_3. Thus affinities with this genus and subfamily can be excluded. Furthermore, the validity of this fossil subfamily remains debatable.

According to the key to Nearctic tanypodine tribes and genera of Oliver (1981) and to Fittkau (1962), *Libanopelopia* gen. n. falls in the Pentaneurini because of the following characters: fourth tarsomeres cylindrical, not cordiform; cubital fork proximal to cross-vein MCu; costa produced beyond the radius by distance less than length of cross-vein RM; postanepisternal setae absent; postnotal setae absent; tibial spurs of hind legs not flattened. However, there are no recent Pentaneurini which bear the configuration of the R veins found in *Libanopelopia*. Apart from the short costal extension, the overall wing venation conforms to the tribe Macropelopiini, particularly in the shape of radial veins. The costal extension is quite variable and obviously less important than the overall wing venation. We thus consider the possibility of the genus belonging to the tribe Macropelopiini.

In the keys to Tanypodinae by Murray and Fittkau (1989) and Sæther *et al.* (2000), *Libanopelopia* keys to couplet 32 and couplet 44 respectively, since vein MCu is placed beyond FCu, the costa is produced beyond the radius by a distance less than the length of RM and ending slightly before M_{1+2}, the gonostylus is short, volsellae appear to be absent, the gonostylus is not robust and has parallel sides, the claws are not spatulate, and the eyes are bare. Included in couplet 32 are the pentaneurine genera *Zavrelimyia* Fittkau, 1962, *Reomyia* Roback, 1987, *Krenopelopia* Fittkau, 1962 and *Telmatopelopia* Fittkau, 1962 (Roback 1987). However, unlike *Libanopelopia,* all these genera have a reduced R_2, and veins R_1 and R_{2+3} are very closely parallel. In addition, *Zavrelimyia* has an indistinct R_3 which does not reach the costa. *Reomyia* has a scutal tubercle and a gonostylus which is not strongly curved. In *Krenopelopia,* the costa ends above or slightly beyond M_{1+2} and the gonostylus is about three quarters the length of the gonostylus. *Telmatopelopia* has a gently curved gonostylus but otherwise, among the species included in couplet 32, it appears to be the genus most similar to *Libanopelopia.*

If the short costal extension is disregarded, *Libanopelopia* keys to the macropelopiine genus *Derotanypus* Roback, 1971 (Murray & Fittkau 1989; Sæther *et al.* 2000), since vein MCu is placed beyond FCu, the tibial spurs have lateral teeth, the postnotals are absent and tibial combs are present only on the hind legs. *Libanopelopia* differs from the genus *Derotanypus* Roback, 1971 in the presence of a shorter costal extension and an unequal length of the tibial spurs.

Tribe Pentaneurini Hennig, 1950

Genus **Cretapelopia** gen. n.

Etymology: After Cretaceous and *Pelopia*.

Type species: *Cretapelopia salomea* sp. n., by present designation.

Diagnosis: Postnotum with numerous long setae and a very distinct longitudinal median groove; scutal tubercle absent; scutellum with numerous long setae. Costa ending just beyond the apex of R_{4+5}, not produced well beyond it, almost reaching wing apex opposite to apex of M_{1+2}; R_2 very short, and veins R_1 and R_{2+3} very closely parallel. Apical brush of strong setae on tarsomere 3 of mid leg absent; all tibial spurs very long and of subequal length, with lateral comb-like teeth. Distal half of gonostylus straight and tapering at apex; anal point sharp and long; gonocoxite rounded.

Cretapelopia salomea sp. n.

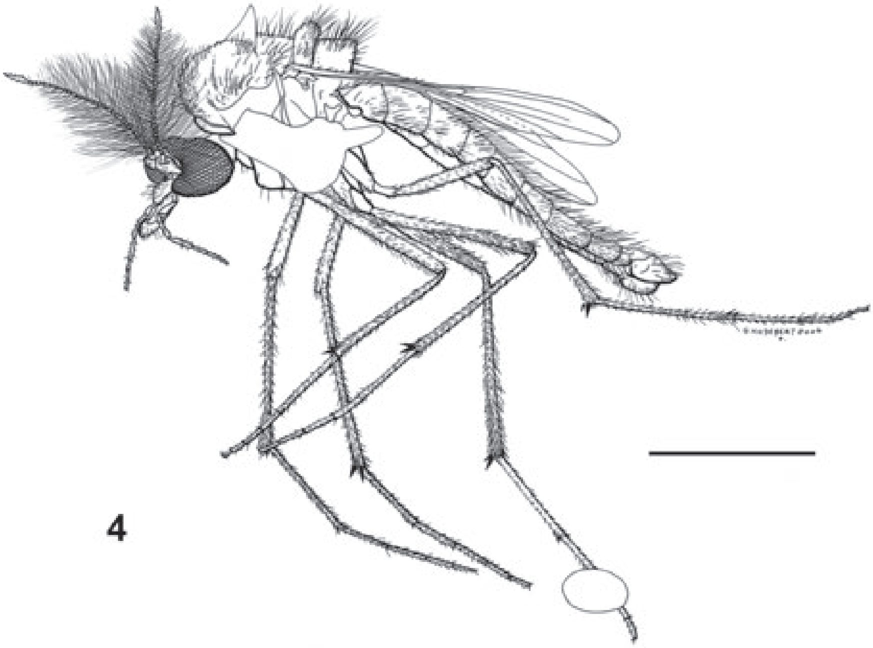
Figs 4–6

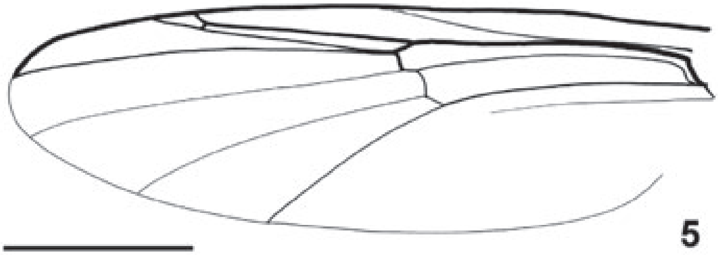
Etymology: After Salomé, daughter of one of the authors (I.V.).

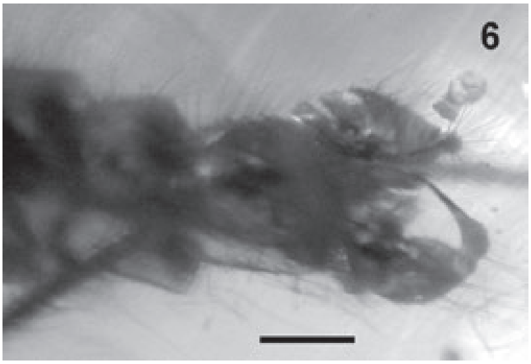
Description: Head 0.82 mm long, 0.55 mm wide. Ocelli absent. Antenna 1.2 mm long, much longer than head, distinctly hairy, 14 flagellomeres; flagellomeres 1–13 covered with long setae (shortest 0.04 mm long, longest 0.5 mm long), scape broad and short, rounded, pedicel very short, flagellomere 13 very long (0.1 mm), flagellomere 14 evenly tapering from base to apical nipple, 0.17 mm long, 9 times as long as broad at base. Eye bare, deformed but with an apically-expanded dorso-medial extension, with 7 rows of ommatidia at minimum width. Clypeus 0.13 long with few dorsal setae. Mouthparts lacking functional mandible, labium 0.39 mm long; palpomeres with numerous setae, all approximately the same length. A row of short postocular setae; frontal, inner vertical and outer vertical setae not visible.

Thorax 1.14 mm long, 0.64 mm wide, 0.84 mm high; postnotum with numerous long setae and very distinct longitudinal median groove; numerous prealar and supraalar setae; series of about 10 anterior acrostichals; series of few poorly aligned dorsocentrals; postanepisternal setae present.

Wing macropterous, 2.32 mm long, 0.65 mm wide, hyaline, and covered with macrotrichia. Radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_{2+3} well separated from R_1 and R_{4+5}, R_{2+3} apically forked into R_2 and R_3; R_2 0.06 mm long, ending in R_1, R_3 0.16 mm long, ending in costa. Costa produced beyond insertion of last radial branch by 0.04 mm, distinctly shorter than cross-vein RM. Only M_{1+2} and M_{3+4} present; cross-vein







Figs 4–6. *Cretapelopia salomea* gen. et sp. n., holotype 309: (4) details of general habitus, scale bar = 1 mm; (5) wing, scale bar = 0.5 mm; (6) male genitalia, scale bar = 0.2 mm.

MCu present; cubital fork proximal to cross-vein MCu; cross-vein RM 0.03 mm slightly distal of MCu. Anal vein An_2 absent. Halter 0.36 mm long.

Fore femur length 0.82 mm, tibia 1.1 mm, tarsus 1.8 mm; mid femur 1.14 mm, tibia 1.08 mm, tarsus 1.34 mm; hind femur 1.04 mm, tibia 1.08 mm, tarsus 1.26 mm. Tibial spur formula 1–2–2; all spurs 0.08 mm long, with lateral comb-like teeth, (similar to those of extant genus *Derotanypus*). Fourth tarsomeres of all legs cylindrical, not cordiform; claw of middle legs simple as in fore and hind legs, not pectinate; no apical brush on tarsomere 3 of middle leg.

Abdomen 2.26 mm long, 0.8 mm wide. Gonostylus strongly curved at base (base width 0.06 mm), with numerous long, strong setae, and distally very long (0.16 mm), straight, nearly as long as gonocoxite and tapering at apex; gonocoxite rounded, (0.2 mm long, 0.15 mm wide), with numerous long setae. Anal point sharp and long, 0.1 mm wide at base, 0.02 mm high. Inferior volsella apparently rounded, covered with setae.

Holotype: Specimen 309, male. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana / Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Paratype: Specimen 295, male, same data as holotype.

Discussion: *Cretapelopia* gen. n. appears to fall into the tribe Pentaneurini (Tanypodinae) for the same reasons as *Libanopelopia* (see above). However, it differs from the latter genus in having very reduced R_2, with veins R_1 and R_{2+3} very closely parallel, thus being in accordance with the wing venation of the Pentaneurini.

In the Tanypodinae keys (Murray & Fittkau 1989; Sæther *et al.* 2000) this new genus keys to couplets 6 and 24 respectively. It will not key further since the costal extension is short while postnotals are present. Disregarding the postnotals, the genus keys to couplets 24 and to *Pentaneura* Philippi, 1865 respectively because of the following characters: vein MCu placed beyond FCu, costa not produced; inferior volsella apparently present and rounded in shape; gonostylus broad and strongly curved at base, but distally long, straight and tapering apically; anal point broader than long; scutal tubercle absent; tibia of middle leg bearing two spurs of equal length; tibial spur formula 1–2–2. The tibial spurs of *Cretapelopia* are very different from those of *Pentaneura* (see Murray & Fittkau 1989). In couplet 24, genera without a scutal tubercle, *Rheopelopia* Fittkau, 1962, *Thienemannimyia* Fittkau, 1962, *Meropelopia* Roback, 1971, and *Arctopelopia* Fittkau, 1962, lack postnotals or anepisternals. In these genera, the costa ends approximately opposite to the apex of M_{1+2}, but R_3 ends almost halfway between R_1 and R_{4+5}. Among the Tanypodinae, only some Anatopyniini and Macropelopiini have postnotals or anepisternals; present in *Cretapelopia*. However, judging from the distribution of the thoracic chaetotaxy in the Orthocladiinae, both basal and advanced genera may have these setae and, at least among the orthoclads, this character appears to be of low phylogenetic value.

Tribe Anatopyniini Fittkau, 1962

Genus **Wadelius** gen. n.

Etymology: After Jean-Marc Wadel, friend of one of the authors (I.V.).

Type species: *Wadelius libanicus* sp. n., by present designation.

Diagnosis: Fourth tarsomere cyclindrical, as long as fifth tarsomere; robust and curved claw-like tibial spurs with no lateral teeth; row of long and rigid setae on inner side of all femora. R_{2+3} apically divided into R_2 and R_3, with R_2 rather long and well distinct; costa produced slightly distal to apex of R_{4+5}; cubital fork slightly proximal to cross-vein MCu. Postanepisternal and postnotal setae present; scutal tubercle present; pulvilli absent; vertical and postorbital setae uniserial. Gonostylus nearly bare, bifurcated in two equally long and slightly curved appendages, the inner appendage ending in a gonostylar tooth; inferior volsella not visible, if present, very small.

Wadelius libanicus sp. n.

Figs 7, 8

Etymology: After Lebanon.

Description: Head 0.25 mm long, 0.52 high. Ocelli absent. Antenna 0.8 mm long, more than 3 times longer than head, distinctly hairy, with 14 flagellomeres, flagellomeres 1–13 covered with long setae (shortest 0.05 mm long, longest 0.4 mm long), scape broad and short, rounded, pedicel very short, flagellomere 13 long (0.3 mm), flagellomere 14 evenly tapering from base to apical nipple, 0.09 mm long. Eye bare, with apically expanded dorso-medial extension. Clypeus 0.13 mm long, with few dorsal setae. Mouthparts lacking functional mandible; all palpomeres with numerous setae; labium 0.23 mm. Uniserial postocular setae; numerous long frontal setae visible; inner vertical and outer vertical setae not visible.

Thorax 0.93 mm long, 0.92 mm high; antepronotum bare; postnotum bearing long setae and with longitudinal groove; scutal tubercle present; scutellum with broken setae; numerous acrostichals, supraalar and prealar setae; postanepisternal setae present.

Wing macropterous, 1.6 mm long, 0.42 mm wide, hyaline, covered with macrotrichia. Costa ending just beyond insertion of last branch of radius, produced by 0.06 mm, shorter than cross-vein RM. Radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_{2+3} well separated from R_1 and R_{4+5}, R_{2+3} clearly visible at base and apex but evanescent in its main part; R_2 0.02 mm long, ending in R_1, R_3 0.15 mm long, ending in costa. Only M_{1+2} and M_{3+4} present; cross-vein MCu present. Cubital fork 0.05 mm proximal to cross-vein MCu; cross-vein RM 0.02 mm distal of MCu. Anal vein An_2 absent. Halter 0.2 mm long.

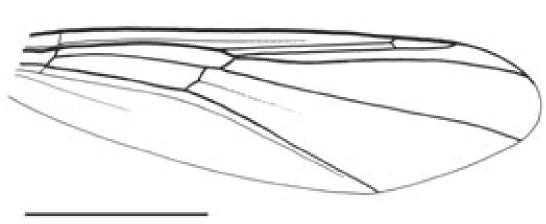
Fore femur length 0.7 mm, tibia 0.82 mm, tarsus 1.08 mm; mid femur 0.7 mm, tibia 0.84 mm, tarsus 0.96 mm; hind femur 0.6 mm, tibia 0.86 mm, tarsus 1.22 mm. Tibial spur formula 1–2–2, with no lateral teeth; two robust and curved claw-like spines on tibial end, 0.04 mm long; hind tibial comb disposed in one row. Fourth tarsomeres of all legs cylindrical, not cordiform; claw simple, not pectinate.

Abdomen 1.4 mm long, 0.4 mm wide. Gonostylus 0.15 mm long; gonocoxite 0.22 mm long, 0.15 mm wide at base, with numerous long setae. Anal point very smooth and broad, though small; 0.04 mm wide at base, 0.05 mm high.

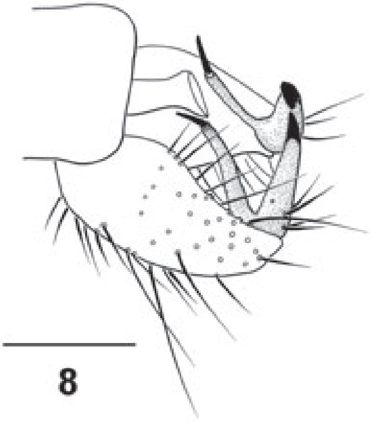
Holotype: Specimen 748A, male. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana / Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Paratype: Specimen 259 (male), same data as holotype.

Discussion: This peculiar tanypodine may deserve a separate tribe. However, one of the most distinct and unique synapomorphies within the Tanypodinae is the comb-like formation of the tibial spurs. The only recent tanypodine without such tibial spurs belongs



7



8

Figs 7, 8. *Wadelius libanicus* gen. et sp. n.: (7) wing, holotype 748A, scale bar = 0.5 mm; (8) male genitalia, paratype 259, scale bar = 0.1 mm.

to the tribe Anatopyniini with the single included genus *Anatopynia* Johannsen, 1905. Similarities between *Wadelius* and this tribe also are found in the extensive thoracic chaetotaxy and in the probable absence of an inferior volsella. The wing venation is also similar although the costa is more produced and the cubital fork is more proximal to cross-vein MCu in *Anatopynia*. In addition, unlike *Anatopynia, Wadelius* has a scutal tubercle.

The two genera *Tanypus* Meigen, 1803 and *Nilotanypus* Kieffer, 1923 have very rudimentary comb-like structures, which are very difficult to see. *Wadelius* has similar tibial spurs, but it differs from the former genus in the MCu and cubital fork position, and from the latter in the presence of a divided R_{2+3}. We tentatively attribute *Wadelius* to the Anatopyniini.

Subfamily Orthocladiinae Kieffer, 1911 (see Spies 2005)

Genus **Lebanorthocladius** gen. n.

Etymology: After Lebanon and recent genus *Orthocladius*.

Type species: *Lebanorthocladius furcatus* sp. n., by present designation.

Diagnosis: The genus differs from all other Orthocladiinae in having the following set of characters: wing bare with anal lobe not produced, bare squama, scutal tubercle present, low venarum ratio, very short costal extension, R_{4+5} ending opposite to apex of M_{3+4}, straight Cu_1, large triangular anal point, furcate gonostylus, and hind tibia with one spur only.

Lebanorthocladius furcatus sp. n.

Figs 9–12

Etymology: After the forked gonostylus, characteristic of the male.

Description: Head 0.12 mm long. Ocelli absent. Antenna 0.56 mm long, almost 5 times length of head, distinctly hairy, with 13 flagellomeres covered with long setae (shortest 0.04 mm, longest 0.2 mm), scape broad and short, rounded, pedicel very short,

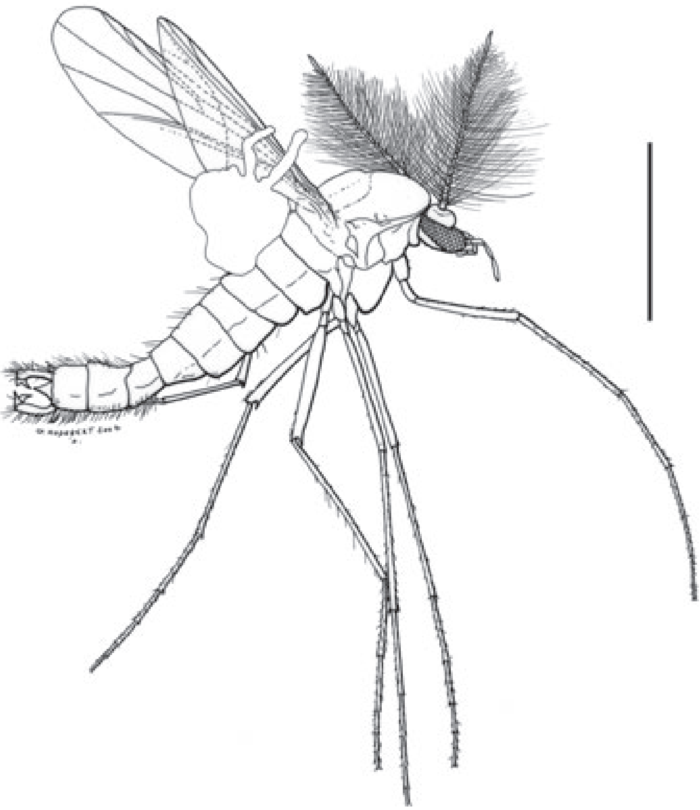
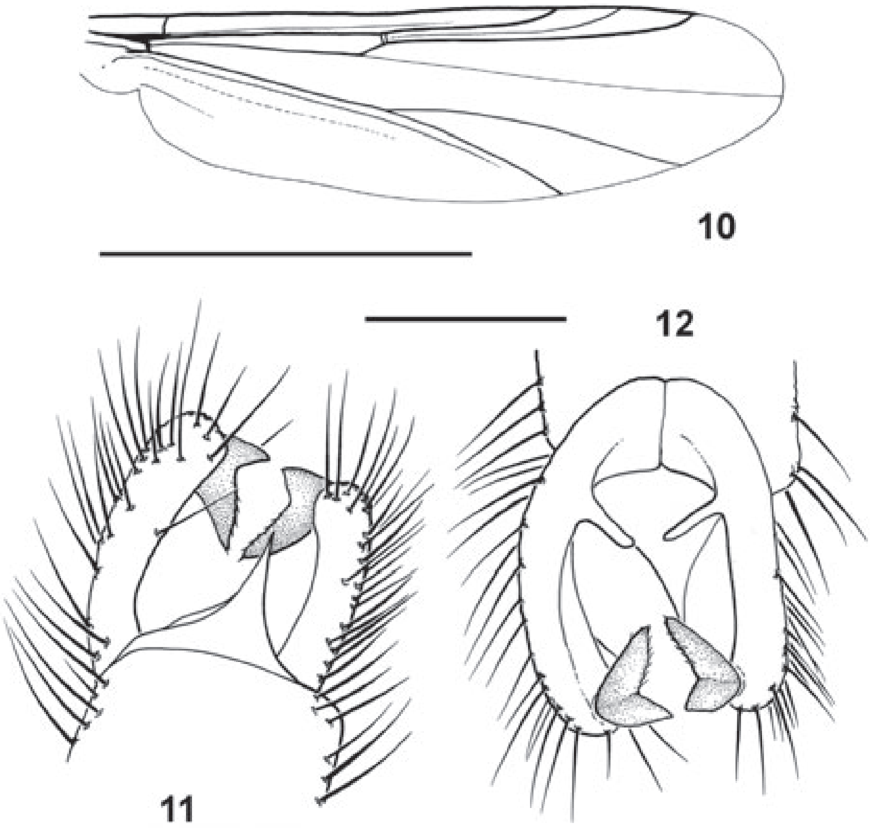


Fig. 9. *Lebanorthocladius furcatus* gen. et sp. n., holotype 5B, general habitus, scale bar = 0.5 mm.

flagellomere 13 very long (0.07 mm). Eye bare, with a small dorso-medial extension, with 3 rows of ommatidia at minimum width. Clypeus with few dorsal setae. Mouthparts lacking functional mandible; 4 palpomeres with numerous setae, all of approximately the same length. Postocular, frontal, inner vertical and outer vertical setae not visible, possibly absent.

Thorax 0.46 mm long, 0.38 mm high; postnotum without visible setae, and no visible longitudinal median groove; surface of scutellum without visible setae; acrostichals and dorsocentrals not visible, probably absent; scutal tubercle present; scutum without median longitudinal groove; epimeron II, posterior mesanepisternum II and dorsal antepronotum bare; no lanceolate setae on scutum; antepronotal lobes not widely separated; anapleural suture distinct.

Wing macropterous, 0.84 mm long, 0.26 mm wide, hyaline, membrane bare. Costa ending just beyond insertion of last branch of radius, distinctly shorter than cross-vein RM. Radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_{2+3} well separated from R_1 and R_{4+5}, R_{2+3} not forked into R_2 and R_3, ending in costa; R_1 and R_{4+5} elongate, separated from costa until apex; area between costa and R_{4+5} broad. Only M_{1+2} and M_{3+4} present; cross-vein MCu absent; Cu_1 nearly straight. Anal vein An_2 absent; squama without setae. Halter 0.12 mm long.



Figs 10–12. *Lebanorthocladius furcatus* gen. et sp. n., holotype 5B: (10) wing, scale bar = 0.5 mm; (11, 12) dorsal and ventral aspects of male genitalia, scale bar = 0.1 mm.

Fore femur length 0.34 mm, tibia 0.36 mm, tarsus 0.62 mm; mid femur 0.34 mm, tibia 0.44 mm, tarsus 0.5 mm; hind femur 0.38 mm, tibia 0.48 mm, tarsus 0.6 mm. All tarsomeres of fore, middle and hind legs cylindrical, not cordiform; first tarsomere of fore leg distinctly shorter than fore tibia. Hind tibia with one spur and a comb comprised of basally separated spines. Fore coxa not enlarged.

Abdomen 1 mm long, 0.16 mm wide. Gonostylus hinged to gonocoxite and folded inward; short and bifurcate. Gonocoxite with numerous long setae, elongate. Superior (?) volsella large, digitiform; no median volsella and no apparent inferior volsella. Anal point sharp and long, 0.4 mm wide at base, 0.07 mm high.

Holotype: Specimen 5 B, male. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana / Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Other material studied: Specimen 574 I, male, with genital organs missing, from the same locality and possibly also belonging to this species.

Discussion: This species belongs to the subfamily Orthocladiinae because of the following characters: wing present; cross-vein MCu absent; first tarsomere of fore leg distinctly shorter than fore tibia; hind tibia with one spur and a comb comprised of basally separated spines; gonostylus hinged to gonocoxite and folded inward;

antepronotal lobes not widely separated; fore coxa not enlarged; anapleural suture distinct (Oliver 1981; Oliver & Dillon 1989). Except for the key to Holarctic genera of Cranston *et al.* (1989), and the key to Palaearctic genera in Sæther *et al.* (2000), there is no recent world revision of the orthocladiine genera.

Few recent genera have a double, forked, or broad triangular gonostylus, as in *Lebanorthocladius* gen. n., viz. *Aagaardia* Sæther, 2000, *Brillia* Kieffer, 1913, *Diplosmittia* Sæther, 1981, *Plhudsonia* Sæther, 1982, *Propsilocerus* Kieffer, 1923 (= *Tokunagayusurika* Sasa, 1978), *Zalutschia* Lipina, 1939, some *Chaetocladius* Kieffer, 1911, some *Parachaetocladius* Wülker, 1959, and one *Orthocladius* van der Wulp, 1847. *Brillia*, *Diplosmittia*, *Plhudsonia* and *Propsilocerus* have a double gonostylus. *Lebanorthocladius* differs from all of the other genera by the following combination of characters: straight Cu_1, very short costal extension, and R_{4+5} ending opposite to apex of M_{3+4}. All genera except *Aagaardia* also have setae on squama and all lack a scutal tubercle. The volsellae are of the type found in the *Brillia* group of genera, present, for instance, in *Eurycnemus* van der Wulp, 1874 (Fittkau 1974; Sæther 1982, 2000*b*; Chaudhuri & Bhattacharyay 1989; Cranston *et al.* 1989; Kawai 1991; Kobayashi & Sasa 1991; Niitsuma 1991; Sæther & Wang 1992, 1996; Andersen & Sæther 1993*a*, *b*; Sæther & Andersen 1993, 1995; Sæther & Ferrington 1993; Kobayashi 1994; Boothroyd 1994, 1999; Boothroyd & Cranston 1994; Epler & de la Rosa 1995; Ferrington & Sæther 1995; Oliveira *et al.* 1995; Sæther & Kristoffersen 1996; Harrison 1997, 2000; Wiedenbrug & Fittkau 1997; Wang & Sæther 1998, 2002; Cranston & Edward 1999; Sæther & Ekrem 1999; Yamamoto 1999; Cranston 2000; Maheshwari & Maheshwari 2001; Mendes *et al.* 2004*a*, *b*).

Subfamily Podonominae Thienemann & Edwards, 1937

Genus *Libanochlites* Brundin, 1976

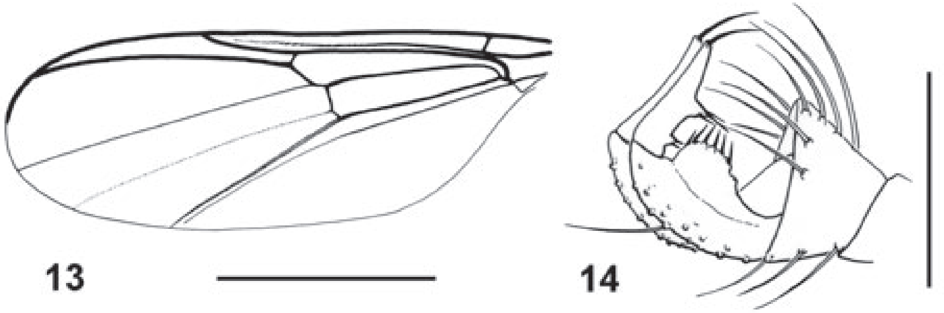
Libanochlites neocomicus Brundin, 1976

Figs 13, 14

Description: Head 0.22 mm long. Ocelli absent. Antenna 0.5 mm long, more than twice as long as head, distinctly hairy, with 14 flagellomeres. Flagellomeres 1–13 covered with long setae (shortest 0.01 mm, longest 0.32 mm), scape broad and short, rounded, pedicel very short. Flagellomere 13 very long (0.07 mm); last 2 flagellomeres slightly more than half as long as remainder of flagellum. Flagellomere 14 long, tapering evenly/consistently from base to apical nipple, less than half as long as flagellomere 13. Eye bare, with a distinct dorso-medial extension. Mouthparts lacking functional mandible; palps very short, with 4 visible palpomeres bearing numerous setae, all of similar length. Postocular, frontal, inner vertical and outer vertical setae not visible; possibly absent.

Thorax 0.48 mm long, 0.25 mm wide, 0.27 mm high; postnotum with few setae, and no visible longitudinal median groove; scutellum with few posterior setae; scutum without median longitudinal groove; dorsal antepronotum with several setae.

Wing macropterous, 0.70 to 0.82 mm long, 0.22 mm wide, hyaline; membrane with setae. Radius with only 2 branches R_1 and R_{4+5}; R_1 short, 0.4 times as long as R_{4+5}. Costa with very long free end, distal of apex of R_{4+5}; cell between R_{4+5} and costa narrow. Cross-vein MCu present, just proximal of RM; fork of Cu just proximal of MCu; Cu_1 not curved apically. Anal vein An_2 absent. Halter 0.1 mm long.



Figs 13, 14. *Libanochlites neocomicus* Brundin, 1976, male, specimen 723: (13) wing, scale bar = 0.3 mm; (14) genitalia, scale bar = 0.1 mm.

Fore femur length 0.44 mm, tibia 0.47 mm, tarsus 0.57 mm; mid femur 0.44 mm, tibia 0.5 mm, tarsus 0.73 mm; hind femur 0.44 mm, tibia 0.49 mm, tarsus 0.76 mm. All tarsomeres of fore, middle and hind legs cylindrical, not cordiform; first tarsomere of fore leg very long, but shorter than fore tibia. Mid and hind tibias with 2 spurs; claw of middle legs simple as in front and hind legs, not pectinate.

Abdomen 1 mm long, 0.07 mm wide. All tergites with 2 long dorsal setae; laterosternite IX fused with tergite IX. Gonostylus swollen at base and extended into a long, slender lobe with a sharp apical spine. Gonocoxite broad, with numerous long setae, elongate.

Material examined: LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Specimens 236, 80, 179, 221, 250 A, 382, 940, 1148, 748 B (9♂), 511, 537, 538, 781 A and B, 1111, 1272B (7♀) and 723 G, H, I , J (1♀, 3♂) from Hammana/Mdeyrij, Caza Baabda (D. Azar coll.). *South Lebanon district* [*Mouhafazit Loubnan el-Janoubi*]: JG 375/3 BM 497, JG 375/5 BM 467 (2♀), JG 375/1 BM 496 (♂) from Jouar Es-Souss (Jezzine outcrop) (Acra coll.). *North Lebanon district*: DAB 6 B (♂) from El-Dabsheh (D. Azar coll.).

Discussion: The male and female specimens examined have the same wing venation as the unique female holotype of *L. neocomicus*, from the outcrop of Jouar Es-Souss near Jezzine, usually known as Jezzine outcrop. The only differences are due to sexual dimorphism (number and structures of the antennomeres, size of the eyes, length of wings). Also the new male specimen (JG 375/1 BM 496) from Jezzine has the same genitalia as those from Hammana. Therefore, we consider that they belong to the same genus and species. The allocation of *Libanochlites* to the subfamily Podonominae was initially based on rather unimportant characters (Brundin 1976). However, the recent discovery of the male has allowed for a more detailed examination of the primary characters, which further supports the position of *Libanochlites* within the Podonominae.

Following the key to Holarctic subfamilies of Oliver and Dillon (1989), *Libanochlites* could fall within the Podonominae or the Buchonomyiinae. However, the laterosternite IX fused with tergite IX in *Libanochlites* is an apomorphy of the group Tanypodoinae and thus excludes affinities with the Buchomomyiinae (Brundin & Sæther 1978; Sæther 2000*a*). Despite having a wing venation very similar to that of *Libanochlites*, the Chilenomyiinae have distinctly different male genital structures (laterosternites IX, gonostyli) (Brundin 1983).

Within the Tanypodoinae, affinities with the Usambaromyiinae can be excluded because of the following characters: presence of vein MCu; tarsomere 4 elongate, not cordiform; claw of middle legs simple as in front and hind legs, not pectinate (Andersen & Sæther 1994). Affinities with the Tanypodinae can be excluded because of the absence of vein R_{2+3}. Brundin (1976) indicated that this character is an apomorphy of the Podonominae, while the other character—an obsolete anal lobe—is also shared by *Libanochlites*. The Aphroteniinae, the last tanypodoine subfamily, can be excluded because within *Libanochlites,* vein MCu is retained; a character apomorphically absent in the Aphroteniinae. *Libanochlites* also has a narrow cell between R_{4+5} and the costa, an apomorphy absent in the recent Aphroteniinae, but present in Podonominae (Brundin 1966, 1976). The simple gonostylus of *Libanochlites* excludes affinities with the Podonomini and justifies allocation to the Boreochlini, after the female characters, already indicated by Brundin (1976). The most similar recent genus is *Paraboreochlus* Thienemann, 1939, since cross-vein MCu is proximal to cross-vein RM, the pulvilli are not visible and thus probably absent, the tibial spurs are slender, and the eyes are bare (Brundin 1966, 1976; Cranston *et al.* 2002). The broad gonocoxites and narrow elongate gonostyli of *Libanochlites* are also similar to those of this recent genus and yet very different from those of the other recent genera (Brundin 1989). Brundin (1976) separated *Paraboreochlus* from *Libanochlites* based on small differences in the wing venation. In *Paraboreochlus*, R_1 is comparatively longer, the wing itself is slightly longer, and the relative position of MCu with fork of Cu differs from *Libanochlites*. In addition, the male gonostylus of *Paraboreochlus* has small apical megaseta while in *Libanochlites*, the gonostylus has a sharp apical spine.

Subfamily Prodiamesinae Sæther, 1976

Genus **Libanodiamesa** gen. n.

Etymology: After Lebanon and *Diamesa*.

Type species: *Libanodiamesa deploegi* sp. n., by present designation.

Diagnosis: R_{2+3} present, simple. MCu present, in a very basal position, midway between base of M and RM; FCu distal to MCu. Wing membrane without setae. Eye bare.

Libanodiamesa deploegi sp. n.

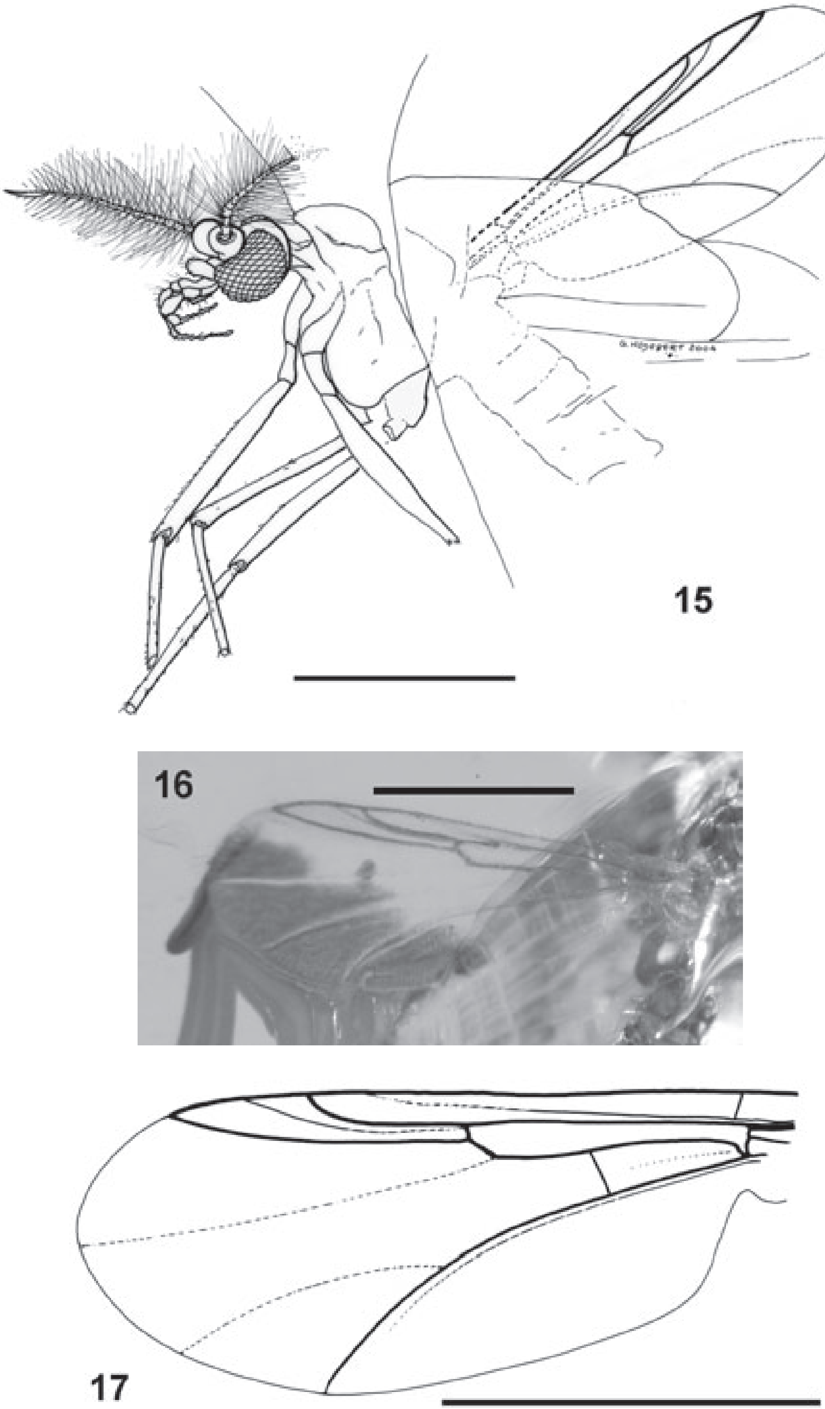
Figs 15–17

Etymology: After Mr Gaël De Ploeg who with great talent, helped in preparing the material for study.

Description: Head 0.26 mm long. Ocelli absent. Antenna 0.5 mm long, almost twice as long as head, distinctly hairy, with 13 flagellomeres, all covered with long setae (shortest 0.04 mm, longest 0.18 mm). Scape broad and short, rounded; pedicel very short. Eye bare, with distinct dorso-medial extension. Mouthparts lacking functional mandible; palps long, with four visible palpomeres bearing numerous setae, last palpomere the narrowest and longest. Two postocular setae; frontal, inner vertical and outer vertical setae not visible, possibly absent.

Thorax 0.8 mm long, 0.6 mm wide, 0.8 mm high. Postnotum, scutellum, scutum without visible setae.

Wing macropterous, 1.2 mm long, 0.41 mm wide, hyaline; membrane without setae. Costa ending at apex of R_{4+5}; radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_1 rather long, 1.66 times as long as R_{4+5}; R_{2+3} simple, closely aligned and parallel to R_1. Cross-vein MCu present, in a very basal position, about midway between base of M and RM.



Figs 15–17. *Libanodiamesa deploegi* gen. et sp. n., holotype 66: (15) general habitus; (16) forewing; (17) details of forewing venation. Scale bars = 0.5 mm.

Fork of Cu nearly opposite RM; Cu_1 curved. Anal vein An_2 absent. Halter 0.14 mm long.

Fore femur length 0.46 mm, mid femur 0.5 mm, hind femur 0.44 mm.

Abdomen narrow, 0.2 mm wide.

Holotype: specimen 66, all tibiae apically broken, tibial spurs destroyed, tarsi missing, apex of abdomen destroyed. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana / Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Discussion. Following the key to Holarctic subfamilies of Oliver and Dillon (1989) and to Palaearctic subfamilies in Sæther *et al.* (2000), *Libanodiamesa* gen. n. falls in the Prodiamesinae because of the combination of the following characters: wing macropterous; MCu present; R_{2+3} present, simple; wing membrane without setae; FCu distal to MCu. Furthermore, *Libanodiamesa* has bare eyes, unlike most recent Diamesinae Kieffer, 1923.

Among the non-Holarctic subfamilies, affinities with the Aphroteniinae are excluded because *Libanodiamesa* has retained MCu and R_{2+3}, but it has a narrow space between R_{4+5} and the costa. In the Usambaromyiinae, MCu is absent. The Chilenomyiinae have a MCu in a basal position (less basal than in *Libanodiamesa*), but no R_{2+3}. Furthermore, unlike *Libanodiamesa*, their wings are uniformly covered with dense hair.

Within the Prodiamesinae, *Libanodiamesa* differs from all recent genera in the much more basal position of MCu, located midway between base of M and RM, and in the $R_{4+5,}$ which ends well basad of the wing apex (Sæther 1989). The lack of genital organs in the holotype of *Libanodiamesa* renders it impossible to predict the relationship of this genus with the other recent genera. *Libanodiamesa* and *Cretadiamesa* gen. n. (see below) are the oldest representatives of the subfamily Prodiamesinae.

Genus **Cretadiamesa** gen. n.

Etymology: After Cretaceous and *Diamesa*.

Type species: *Cretadiamesa arieli* sp. n., by present designation.

Diagnosis: Closely similar to *Libanodiamesa*; the differences with this genus being as follows: veins R_1 and R_{4+5} strongly approximate; R_{2+3} very weakly indicated; apex of R_{4+5} near wing apex; costa ending near wing apex.

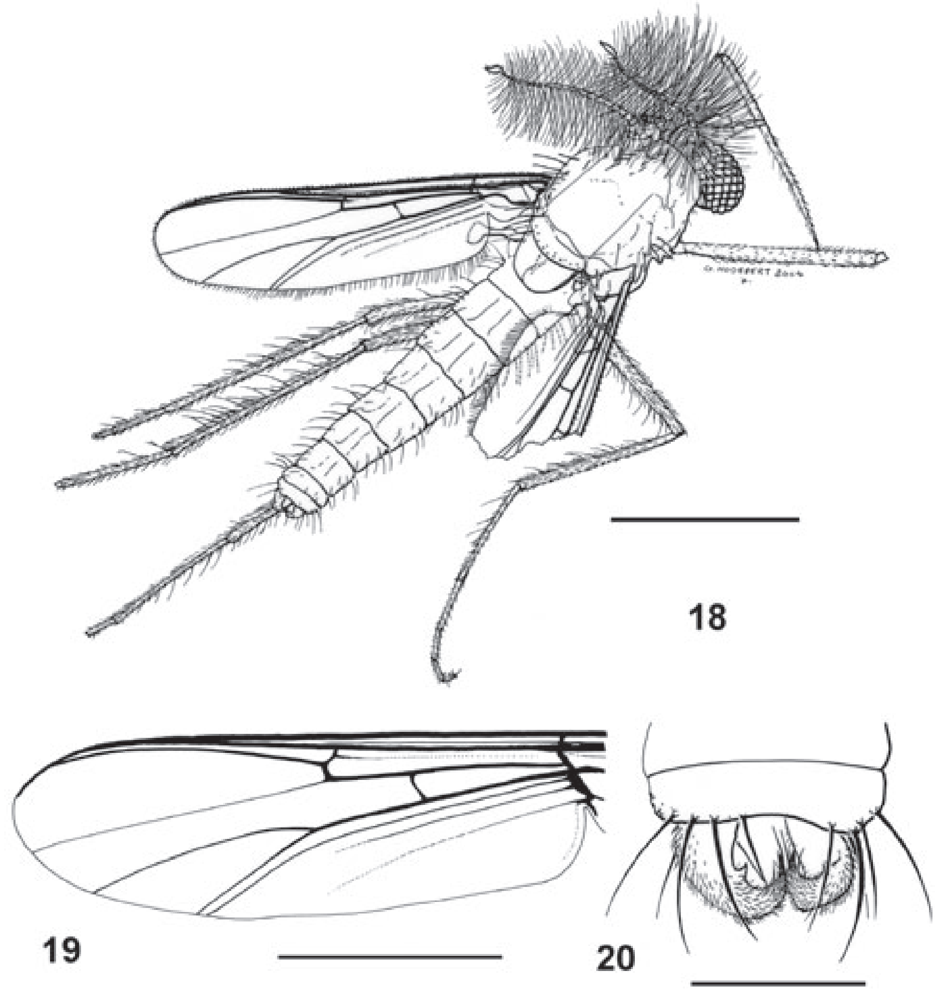
Cretadiamesa arieli sp. n.

Figs 18–20

Etymology: After Ariel, son of one of the authors (I.V.).

Description: Head 0.2 mm long. Ocelli absent. Antenna 0.6 mm long, 3 times the length of the head, distinctly hairy, with 13 flagellomeres, all covered with long setae (shortest 0.02 mm, longest 0.4 mm). Scape broad and short, rounded; pedicel very short. Eye bare, with a distinct dorso-medial extension. Mouthparts lacking functional mandibles; palps long, with 5 palpomeres bearing numerous setae, all approximately the same length. Two postocular setae; frontal, inner vertical and outer vertical setae not visible, possibly absent.

Thorax 0.5 mm long, 0.36 mm wide, 0.1 mm high. Postnotum and scutellum with few, rather short setae. Scutum with a central group of acrostichals and 2 lines of sparse dorsocentrals.



Figs 18–20. *Cretadiamesa arieli* gen. et sp. n., male, holotype 365: (18) general habitus, scale bar = 0.5 mm; (19) wing, scale bar = 0.3 mm; (20) details of male genitalia, scale bar = 0.1 mm.

Wing macropterous, 1.1 mm long, 0.3 mm wide, hyaline, membrane without setae. Costa ending at apex of R_{4+5}, near wing apex. Radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_1 rather long, 3 times as long as R_{4+5}; R_{2+3} simple, closely aligned and parallel to R_1 but very weakly indicated; R_1 and R_{4+5} strongly approximate. Cross-vein MCu present in a very basal position, approximately midway between base of M and RM. Fork of Cu nearly opposite RM; Cu_1 weakly curved. Anal vein An_2 absent. Halter 0.18 mm long.

Fore femur length 0.42 mm; mid femur 0.4 mm; tibia 0.6 mm; hind femur 0.48 mm; tibia 0.66 mm. One hind tibial spur visible, curved; hind tibial comb present, disposed in one row.

Abdomen 0.94 mm long, 0.2 mm wide (male); 0.8 mm long, 0.25 mm wide (female). Male genitalia: abdomen with numerous uniform setae; gonocoxite short and broad;

gonostylus directed upward, curved and short, with an apical megaseta; inferior volsella not visible and thus reduced or absent. Female genitalia: tergite IX undivided; cerci short with small setae; gonocoxites IX not visible.

Holotype: 365, male. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana/Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Allotype: 349, female, same data as holotype.

Discussion: The allocation of the male and female specimens to the same species is based on their similarity in wing venation. Following the key to Holarctic subfamilies of Oliver and Dillon (1989) and to Palaearctic subfamilies in Sæther *et al.* (2000), *Cretadiamesa* gen. n. falls in the Prodiamesinae because of the following characters: macropterous; MCu present; R_{2+3} very weak, but simple; R_1 and R_{4+5} strongly approximate; wing membrane without setae; FCu well distad of MCu. Furthermore, *Cretadiamesa* has bare eyes, unlike in most recent Diamesinae. Among the non-Holarctic subfamilies, affinities with the Aphroteniinae, Usambaromyiinae and Chilenomyiinae are excluded for the same reasons as above. As in *Libanodiamesa, Cretadiamesa* differs from the recent prodiamesine genera in its much more basal position of MCu, midway between base of M and RM.

CONCLUSION

The fossil Chironomidae from the Early Cretaceous Lebanese amber can be attributed to recent subfamilies and, with some uncertainty, to recent tribes. They demonstrate the great antiquity of the chironomid diversity and morphological disparity. Grund (2005) has attempted to use the chironomid subfamily representation in the Cainozoic Dominican amber to infer some palaeoecological data, however he has indicated that such inferences remain speculative. Obviously, there are fewer possibilities to make such inferences for the Early Cretaceous Lebanese amber.

ACKNOWLEDGEMENTS

We would like to thank Mr Gaël De Ploeg for his great help in preparing the material, Gilbert Hodebert for the drawings and Prof. Ibrahim Koubeissy, President of the Lebanese University, for all his help in encouraging the study of Lebanese amber. We also sincerely thank an anonymous referee and Dr O.A. Sæther for their very helpful remarks and corrections.

REFERENCES

ANDERSEN, T. & SÆTHER, O.A. 1993*a*. *Lerheimia*, a new genus of Orthocladiinae from Africa (Diptera, Chironomidae). *Spixiana* **16** (2): 105–112.

———1993*b*. *Colosmittia clavata* gen. n., sp. n., a new orthoclad from the West Usambara Mountains, Tanzania (Diptera: Chironomidae). *Journal of the Kansas Entomological Society* **66** (4): 439–443.

———1994. *Usambaromyia nigrala* gen. n., sp. n., and Usambaromyiinae, a new subfamily among the Chironomidae (Diptera). *Aquatic Insects* **16** (1): 21–29.

ANSORGE, J. 1999. *Aenne liasina* gen. et sp. n. – the most primitive non biting midge (Diptera: Chironomidae: Aenninae subfam. n.) – from the Lower Jurassic of Germany. *Polskie Pismo Entomologiczne* **68**: 431–443.

AZAR, D. 2000. *Les ambres mésozoïques du Liban*. PhD Thesis. Paris: University of Paris-Sud.

BOESEL, M.W. 1937. Diptera. *In*: Carpenter, F.M., Folsom, J.W., Essig, E.O., Kinsey, A.C., Brues, C.T., Boesel, M.W. & Ewing, H.E., eds, *Insects and Arachnids from Canadian Amber, Chironomidae*. *University of Toronto Studies, Geology Series* **40**: 44–55.

BOOTHROYD, I.K.G. 1994. Description of *Naonella* gen. n. (Diptera: Chironomidae: Orthocladiinae). *New Zealand Journal of Zoology* **21** (3): 309–315.

———1999. Description of *Kaniwhaniwhanus* gen. n. (Diptera: Chironomidae: Orthocladiinae) from New Zealand. *New Zealand Journal of Marine and Freshwater Research* **33** (3): 341–349.

Boothroyd, I.K.G. & Cranston, P. 1994. Two Orthocladiinae (Chironomidae) genera common to New Zealand and Australia: *Pirara* gen. n. and *Eukiefferiella* Thienemann. *In*: Cranston, P., ed., *Chironomids: from Genes to Ecosystems*. East Melbourne: CSIRO Publications, pp. 389–408.

Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral *Heptagyiae*. *Kunglica Svenska Vetenskapsakademiens Handlingar* **11**: 1–472.

———1976. A Neocomian chironomid and Podonominae-Aphroteniinae (Diptera) in the light of phylogenetics and biogeography. *Zoologica Scripta* **5**: 139–160.

———1983. *Chilenomyia paradoxa* gen. n., sp. n. and Chilenomyiinae, a new subfamily among the Chironomidae (Diptera). *Entomologica Scandinavica* **14** (1): 33–45.

———1989. The adult males of Podonominae (Diptera: Chironomidae) of the Holarctic region keys and diagnoses. *Entomologica Scandinavica* (Supplement) **34**: 23–36.

Brundin, L. & Sæther, O.A. 1978. *Bruchonomyia burmanica* sp. n., and Bruchonomyiinae, a new subfamily among the Chironomidae (Diptera). *Zoologica Scripta* **7** (4): 269–275.

Chaudhuri, P.K. & Bhattacharyay, S. 1989. *Indocladius*, a new orthocladiid genus from India (Chironomidae). *Reichenbachia* **26** (2): 169–171.

Cranston, P.S. 2000. *Parapsectrocladius*: a new genus of orthocladiinae Chironomidae (Diptera) from Patagonia, the southern Andes. *Insect Systematics & Evolution* **31** (1): 103–120.

Cranston, P.S. & Edward, D.H.D. 1999. *Botryocladius* gen. n.: a new transantarctic genus of orthocladiine midge (Diptera: Chironomidae). *Systematic Entomology* **24** (4): 305–333.

Cranston, P.S., Edward, D.H.D. & Cook, L.G. 2002. New status, species, distribution records and phylogeny for Australian mandibulate Chironomidae (Diptera). *Australian Journal of Entomology* **41**: 357–366.

Cranston, P.S., Oliver, D.R. & Sæther, O.A. 1989. The adult males of Orthocladiinae (Diptera: Chironomidae) of the Holarctic region keys and diagnoses. *Entomologica Scandinavica* (Supplement) **34**: 165–352.

Epler, J.H. & de la Rosa, C.L. 1995. *Tempisquitoneura*, a new genus of Neotropical Orthocladiinae (Diptera: Chironomidae) symphoretic on *Corydalus* (Megaloptera: Corydalidae). *Journal of the North American Benthological Society* **14** (1): 50–60.

Evenhuis, N.L. 1994. *Catalogue of the Fossil Flies of the World (Insecta: Diptera).* Leiden: Backhuys Publishers.

Ferrington, M.C., Jr. & Sæther, O.A. 1995. *Physoneura*, a new genus of Orthocladiinae from Patagonia and South Chile (Chironomiidae). *Aquatic Insects* **17** (1): 57–63.

Fittkau, E.J. 1962. – Die Tanypodinae (Diptera, Chironomidae). Die Tribus Anatopyniini, Macropelopiini und Pentaneurini. *Abhandlungen zur Larvensystematik der Insekten* **6**: 1–453.

———1974. *Ichthyocladius* gen. n., eine neotropische Gattung der Orthocladiinae (Chironomidae, Diptera) deren Larven epizoisch auf Welsen (Astroblepidae und Loricariidae) leben. *Entomologisk Tidskrift* **95** (Supplement): 91–106.

Grund, M. 2005. Chironomids (Diptera: Chironomidae) of Dominican amber. *Ablabesmyia electrohispanolana*, sp. n. and paleoecological indications due to subfamily proportions. *Insect Systematics & Evolution* **36** (1): 29–34.

Harrison, A.D. 1997. Two small Orthocladinae (Chironomidae, Diptera) from the western Cape Province, South Africa. *Annals of the Cape Provincial Museums Natural History* **19** (8): 375–386.

———2000. Four new genera and species of Chironomidae (Diptera) from southern Africa. *Aquatic Insects* **22** (3): 219–236.

Hong, Y.-C., Wang, Z.-B. & Sun, W.-H. 1992. The stratigraphy and fossil insects of Zhongguang basin, Hebei province. *Memoirs of the Beijing Natural History Museum* **51** (3): 20–36.

Kalugina, N.S. 1976. Non-biting midges of the subfamily Diamesinae (Diptera, Chironomidae) from the Upper Cretaceous of Taimyr. *Paleontological Journal* [*Paleontologicheskii zhurnal*] **1**: 78–83. (in Russian)

———1980*a*. Chaoboridae and Chironomidae from the Lower Cretaceous deposits of Manlay. *In*: Kalugina, N.S., ed., *Early Cretaceous Lake Manlay* [*Rannemelovoe ozero Manlay*]. *Transactions of the Joint Soviet-Mongolian Palaeontological Expedition* [*Trudy sovmestnoi Sovetsko-Mongol'skoi paleontologicheskoi ekspeditsii*] **13**: 61–64. (in Russian)

———1980*b*. Cretaceous Aphroteniinae from North Siberia (Diptera, Chironomidae), *Electrokejia brundini* gen. nov., sp. nov. *Acta Universitatis Carolinae Biologica* **1978** (1–2): 89–93.

———1985. Infraorder Psychodomorpha. *In*: Kalugina, N.S. & Kovalev, V.G. *Dipteran Insects of the Jurassic of Siberia* [*Dvukrylye nasekomye yury Sibiri*]. Moscow: USSR Academy of Sciences, pp. 33–113. (in Russian)

———1986. Flies. Muscida (= Diptera). Infraorders Tipulomorpha and Culicomorpha. *In*: Rasnitsyn, A.P., ed., *Insects in the Early Cretaceous Ecosystems of the West Mongolia* [*Nasekomye v rannemelovykh ekosistemakh Zapadnoi Mongolii*]. *Transactions of the Joint Soviet-Mongolian Palaeontological Expedition* [*Trudy sovmestnoi Sovetsko-Mongol'skoi paleontologicheskoi ekspeditsii*] **28**: 112–125. (in Russian)

———1993. Chaoborid and chironomid midges from the Upper Mesozoic of east Transbaikalia. *In*: Ponomarenko, A.G., ed., *Mesozoic Insects and Ostracods of Asia* [*Mezozoiskie nasekomye i ostrakody Azii*]. *Transactions of the Paleontological Institute of the USSR Academy of Sciences* [*Trudy Paleontologicheskogo instituta Akademii nauk SSSR*] **252**: 117–139. (in Russian)

Kawai, K. 1991. Seven new chironomid species (Diptera, Chironomidae) from Japan. *Japanese Journal of Limnology* **52** (3): 161–171.

Kobayashi, T. 1994. Synonymic notes on a genus and a species of the Orthocladiinae (Diptera, Chironomidae) from Japan. *Japanese Journal of Entomology* **62** (4): 745–746.

Kobayashi, T. & Sasa, M. 1991. Description of two new species of the chironomid midges collected from the Tama River, Tokyo (Diptera, Chironomidae). *Japanese Journal of Sanitary Zoology* **42**: 71–75.

Krzemiński, W. & Jarzembowski, E. 1999. *Aenne triassica* sp. n., the oldest representative of the family Chironomidae (Insecta: Diptera). *Polskie Pismo Entomologiczne* **68**: 445–449.

Maheshwari, G. & Maheshwari, G. 2001. Some new Chironomidae from south and middle Andaman Islands, India (Diptera: Chironomidae). *Journal of the Bombay Natural History Society* **98** (3): 406–421.

McAlpine, J.F. 1981. Key to families adult. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., eds, *Manual of Nearctic Diptera*, Volume 1. Monograph 27. Ottawa: Research Branch, Agriculture Canada, pp. 89–124.

Mendes, H.F., Andersen, T. & Sæther, O.A. 2004*a*. New species of *Ichthyocladius* Fittkau, a member of the *Corynoneura*-group (Diptera: Chironomidae: Orthocladiinae), with a review of the genus. *Studies on Neotropical Fauna and Environment* **39** (1): 15–35.

———2004*b*. A review of *Antillocladius* Sæther, 1981; *Compterosmittia* Sæther, 1981 and *Litocladius* new genus (Chironomidae, Orthocladiinae). *Zootaxa* **594**: 1–82.

Murray, D.A. & Fittkau, E.J. 1989. The adult males of Tanypodinae (Diptera: Chironomidae) of the Holarctic region keys and diagnoses. *Entomologica Scandinavica* (Supplement) **34**: 37–123.

Niitsuma, H. 1991. A new genus and species of the primitive Orthocladiinae (Diptera: Chironomidae) from Japan. *Japanese Journal of Entomology* **59** (4): 707–716.

Oliver, D.R. 1981. Chapter 29. Chironomidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., eds, *Manual of Nearctic Diptera*, Volume 1. Monograph 27. Ottawa: Research Branch, Agriculture Canada, pp. 423–458.

Oliver, D.R. & Dillon, M.E. 1989. The adult males of Chironomidae (Diptera) of the Holarctic region – key to subfamilies. *Entomologica Scandinavica* (Supplement) **34**: 11–15.

Oliveira, S.J. de, Messias, M.C. & Ribeiro dos Santos, A. 1995. A new genus and new species of Neotropical Orthocladiinae (Diptera, Chironomidae). *In*: Cranston, P., ed., *Chironomids: from Genes to Ecosystems.* East Melbourne: CSIRO Publications, pp. 409–412.

Roback, S.S. 1987. *Reomyia* a new genus of Tanypodinae-Pentaneurini (Diptera, Chironomidae). *Spixiana* **9** (3): 283–284.

Sæther, O.A. 1982. Orthocladiinae (Diptera: Chironomidae) from SE U.S.A., with descriptions of *Phludsonia*, *Unniella* and *Platysmittia* n. genera and *Atelopodella* n. subgen. *Entomologica Scandinavica* **13** (4): 465–510.

———1989. The adult males of Prodiamesinae (Diptera: Chironomidae) of the Holarctic region keys and diagnoses. *Entomologica Scandinavica* (Supplement) **34**: 155–163.

———2000*a*. Phylogeny of the subfamilies of Chironomidae (Diptera). *Systematic Entomology* **25** (3): 393–403.

———2000*b*. *Aagaardia*, a new Holarctic orthoclad genus (Diptera: Chironomidae). *Aquatic Insects* **22** (3): 177–196.

Sæther, O.A. & Andersen, T. 1993. *Lobosmittia*, a new genus of orthoclads from Tanzania and Turkey (Chironomidae). *Tijdschrift voor Entomologie* **136** (2): 283–287.

———1995. *Ionthosmittia caudiga* gen. n. sp. n., a new orthoclad from the Usambara Mts, Tanzania (Diptera: Chironomidae). *Tropical Zoology* **8** (1): 197–202.

Sæther, O.A., Ashe, P. & Murray, D.E. 2000. Family Chironomidae. *In*: Papp, L. & Darvas, B., eds, *Contributions to a Manual of Palaearctic Diptera (with Special Reference to the Flies of Economic Importance)*. 4 (Appendix A.6). Budapest: Science Herald, pp. 113–334.

Sæther, O.A. & Ekrem, T. 1999. *Molleriella*, a new terrestrial orthoclad genus from the Netherlands (Diptera: Chironomidae). *Acta Zoologica Academiae Scientiarum Hungaricae* **45** (2): 161–168.

SÆTHER, O.A. & FERRINGTON, L.C., JR. 1993. Redescription of *Prosmittia jemtlandica* (Brundin, 1947), with a review of the genus. *Journal of the Kansas Entomological Society* **66** (3): 257–262.

SÆTHER, O.A. & KRISTOFFERSEN, L. 1996. Chironomids with "M-fork". A reevaluation of the *Corynoneura*-group (Insecta, Diptera, Chironomidae). *Spixiana* **19** (2): 229–232.

SÆTHER, O.A. & WANG, X. 1992. *Euryhapsis fuscipropes* sp. n. from China and *Tokyobrillia anderseni* sp. n. from Tanzania, with a review of genera near *Irisobrilla* Oliver (Diptera: Chironomidae). *Annales de Limnologie* **28** (3): 209–223.

———1996. Revision of the orthoclad genus *Propsilocerus* Kieffer (= *Tokunagayusurika* Sasa) (Diptera: Chironomidae). *Entomologica Scandinavica* **27**: 441–479.

SINITSHENKOVA, N.D. 2002. 3.3 Ecological history of aquatic insects. *In*: Rasnitsyn, A.P. & Quicke, D.L.J., eds, *History of Insects*. Dordrecht *etc*.: Kluwer Academic Publishers, pp. 388–426.

SPIES, M. 2005. On selected family-group names in Chironomidae (Insecta, Diptera), and related nomenclature. *Zootaxa* **894**: 1–12.

WANG, X.-H. & SÆTHER, O.A. 1997 (1998). *Qiniella*, a new orthoclad genus from China (Diptera: Chironomidae). *Hydrobiologia* **362**: 103–106.

———2002. *Hanocladius*, a new orthoclad genus from China (Diptera: Chironomidae). *Hydrobiologia* **468** (1–3): 181–183.

WIEDENBRUG, S. & FITTKAU, E.J. 1997. *Oliveiriella almeidai* (Oliveira, 1946), gen. nov., comb. nov., from South America with description of the pupae (Insecta, Diptera, Chiromidae [Chironomidae], Orthocladiinae). *Spixiana* **20** (2): 167–172.

YAMAMOTO, M. 1999. *Trichosmittia hikosana* gen. n. et sp. n. (Diptera: Chironomidae, Orthocladiinae) from Japan. *Journal of the Kansas Entomological Society* **71** (3): 263–271.

ZHANG, J.-F. 1991. New genera and new species of Chironomidae (Diptera, Insecta) from Late Jurassic of China. *Acta Palaeontologica Sinica* **30** (5): 556–569. (in Chinese, with English summary)